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Original Article

Impacts of mussel invasions on the prey preference of two native predators

Lisa Skein[a], Tamara B. Robinson[a], and Mhairi E. Alexander[b]

[a]Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, Private Bag X1, Natural Sciences Building, Merriman Avenue, Stellenbosch, Matieland 7602, South Africa, and [b]Institute of Biomedical and Environmental Health Research (IBEHR), School of Science and Sport, University of the West of Scotland, High Street, Paisley PA1 2BE, UK

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Biotic invasions can result in the displacement of native species. This can alter the availability of native prey and the choices made by native predators. We investigated prey selection by 2 native South African predators, the west coast rock lobster *Jasus lalandii* and the starfish *Marthasterias africana* in response to the invasive mussels, *Mytilus galloprovincialis* and *Semimytilus algosus*, and native mussels, *Aulacomya atra* and *Choromytilus meridionalis*. As the diets of lobsters and starfish are broad and have been suggested to reflect prey availability, we hypothesized that they would consume the most abundant prey, regardless of its native or alien status. Laboratory studies presented predators with varying proportions of native and invasive mussels that represented pre- and post-invasion scenarios. Mussel parameters (shell strength, adductor muscle size, and energy content) that may be of importance in selection by predators were compared among species. Both predators exhibited preference towards the native mussel *C. meridionalis,* even when it was the least abundant prey. The selection of native species occurred despite mussel parameters suggesting that invasive species would be easier to consume. These findings highlight the potential for facilitation of prey invasions, especially when predators avoid alien prey and select for native comparators that may offer resistance to the invasion through inter-specific competition. It is presently unclear how often such a lack of predator-driven biotic resistance acts in combination with indirect facilitation, but interrogating the behaviors that drive such outcomes will advance our understanding of successful invasions.

Key words: **alien species impact, biotic resistance, *Mytilus galloprovincialis*, *Semimytilus algosus*, species interactions.**

INTRODUCTION

Invasions by alien species are occurring globally at an ever increasing rate (Bumbeer and Moreira 2016), a trend that is expected to continue owing to the link between invasions and the expansion of human trade and travel (Harding 2003; Occhipinti-Ambrogi 2007). With the ability to drive biodiversity loss by bringing about changes in habitat (Crooks 1998) and community structure (Grosholz 2002; Sadchatheeswaran et al. 2015), the introduction of alien species can also lead to novel interactions between native and invasive organisms (Freeman and Byers 2006; Alexander et al. 2015a).

Novel interactions occurring between predators and prey (e.g. consumptive or trait-mediated interactions; Werner and Peacor 2003; Jermacz and Kobak 2017) are of particular importance in biological invasions (Sih et al. 2010). However, there is often a focus on the role of invasive predators and their effects on native prey (Carlsson et al. 2009), probably as a result of the impacts of invasive predators being perceived as greater than those resulting from invasive prey (Salo et al. 2007). There is, however, a growing awareness of the role that invasive prey species may have in native systems (Carlsson et al. 2009). Invasive prey often establish in large numbers (Sousa et al. 2009), with the potential to competitively displace native species (Sadchatheeswaran et al. 2015). They may subsequently present a novel food source that, if in high enough abundance, can induce a predatory switch in resource selection in native predators (Sousa et al. 2009). The invasion of round gobies *Neogobius melanostomus* in Lake Erie (USA), for example, was suggested to influence a shift in the prey preference of the native and endangered Lake Erie Water Snake *Nerodia sipedon insularum*, a phenomenon that was attributed to the high abundance of this alien prey (King et al. 2006).

There are instances where such a switch by native predators towards the consumption of invasive prey can invoke biotic resistance (García and Protogino 2005; Sousa et al. 2009; Carlsson et al. 2011; Freestone et al. 2013). Although this can act to limit the abundance and distribution of invasive prey (MacNeil et al. 2013), such switches from feeding on a native resource to a novel, invasive species

Address correspondence to T.B. Robinson. E-mail: trobins@sun.ac.za.

might not occur readily or may not be possible. Indeed, native predators may fail entirely to recognize novel invasive prey organisms as a new or additional food source (Robinson et al. 2015). Even in cases where native predators recognize invasive prey as food, but do not consume it to the same degree as native prey, it could have considerable implications. These can include freeing invasive prey from the predatory pressure normally experienced in its native range and ultimately increasing the probability of successful invasion, as per the enemy release hypothesis (Colautti et al. 2004). The inability of native predators to switch their preferences towards a novel, abundant food source may also result in decreased fitness (e.g. reduced body condition and growth) compared to co-occurring predators that are able to feed extensively on novel prey (Carlsson et al. 2009). Moreover, predators that avoid invasive prey and continue to consume native resources can, to some extent, facilitate invasions of the alien species through the removal of native competitors (i.e. the preferred native prey species; Needles et al. 2015). Switching from familiar to novel prey items has been suggested to occur in generalist predators (Jaworski et al. 2013). Although clear definitions of generalists versus specialists are illusive (Futuyma and Moreno 1988; Vamosi et al. 2014), in the context of predators generalists are most often categorized based on their consumption of various species of prey that often display morphological differences (for example see Hughes and O'brien 2001; Finlay-Doney and Walter 2012; Gianguzza et al. 2016). It is this characterization that we apply in this study.

Marine ecosystems, including estuaries and coastal regions, are considered among the most heavily invaded on earth (Ruiz et al. 1999; Castorani and Hovel 2016), and marine invasive species constitute a serious threat to these native systems. In South Africa there have been a number of prominent marine invasions, and of particular importance has been the establishment of two alien mussels, *Mytilus galloprovincialis* and *Semimytilus algosus* (Grant and Cherry 1985; de Greef et al. 2013). *Mytilus galloprovincialis* has been present along the South African coastline for more than 30 years (Grant and Cherry 1985) with a widespread west and south coast distribution (Robinson et al. 2005). The more recently introduced *S. algosus* was first documented on the west coast in 2009 (de Greef et al. 2013), and spread onto the south coast in ca. 2015. These invasions have occurred at the expense of the native mussels *Aulacomya atra* and *Choromytilus meridionalis*, which have been displaced along many stretches of coastline (Robinson et al. 2007; Sadchatheeswaran et al. 2015). Mussels represent an important food source for various intertidal and subtidal native predators, including whelks, marine birds, starfish, and rock lobsters (Griffiths and Hockey 1987; Caro et al. 2008; Alexander et al. 2015a). It has, therefore, been suggested that the large abundances of *M. galloprovincialis* and *S. algosus* could represent a new food source for marine predators in the region (de Greef et al. 2013). Indeed, the native predatory whelk *Trochia cingulata* has been shown to shift feeding towards invasive mussel species *M. galloprovincialis* and morphologically similar *S. algosus* (Alexander et al. 2015b). However, knowledge of the impacts of these mussel invasions on subtidal predators is lacking and, given a recent range expansion of *S. algosus* onto the south coast, it has become important to determine how subtidal predators in this extended range are responding to this novel prey.

Two subtidal predators that occur along the west and south coast are the west coast rock lobster *Jasus lalandii* and the spiny starfish *Marthasterias africana* formerly misidentified as the European species *Marthasterias glacialis* (Wright et al. 2016). Rock lobsters are considered to have an important role in the structuring of subtidal communities through predation (Tegner and Levin 1983; Barkai and Branch 1988a; Robles et al. 1990; Andrew and Macdiarmid 1991; Babcock et al. 1999; Mayfield et al. 2000a; Blamey and Branch 2012). Although there is evidence of rock lobsters consuming the invasive mussel *M. galloprovincialis*, at least under laboratory conditions (Nicastro et al. 2007), no studies have considered if *S. algosus* has been incorporated into its diet and/or whether its presence has an effect on the selection of prey. Starfish are, similarly, considered important benthic predators that have an impact on a variety of scales, shaping populations and assemblages within their respective communities (Verling et al. 2003; Himmelman et al. 2005). In South Africa, the native starfish *M. africana* has been shown to exhibit a preference toward mussels (Penney and Griffiths 1984). Although it is recognized that species in this genus are capable of exerting strong predation pressure on prey populations (Verling et al. 2003), the majority of studies to date have focused on the importance of predation on intertidal communities (Gaymer et al. 2004). Nonetheless, the impact of starfish in subtidal communities is likely to be even greater in subtidal systems as the environmental stressors characteristic of intertidal habitats (e.g. frequent aerial exposure) no longer play a role (Gaymer et al. 2004). In previous studies, rock lobsters and starfish have been described as generalists (Penney and Griffiths 1984; Mayfield et al. 2000a; Verling et al. 2003), based on their tendency to feed on a large variety of prey (e.g. mussels, winkles, sea urchins, fish, limpets, whelks, barnacles, algae, and sponges; Penney and Griffiths 1984; Mayfield et al. 2000a; Mayfield and Branch 2000), with their diets often reflecting prey availability (Menge 1972; Penney and Griffiths 1984; Mayfield et al. 2000b).

Against this background the aim of this study was 1) to determine the prey preference of *J. lalandii* and *M. africana* when exposed simultaneously to native (*A. atra* and *C. meridionalis*) and invasive (*M. galloprovincialis* and *S. algosus*) mussel prey in a laboratory setting, and 2) to examine how these preferences might vary in a scenario where invasive prey species are most abundant. Based on research conducted prior to the invasions of *M. galloprovincialis* and *S. algosus* (Branch 1978; Griffiths and Seiderer 1980), it was hypothesized that *J. lalandii* and *M. africana* would select for the native mussel *C. meridionalis*, but when offered higher proportions of invasive *M. galloprovincialis* and *S. algosus*, both predators would select for the more abundant alien prey species. The results from this study will offer insight into whether there is potential for biotic resistance against the ongoing invasion of *S. algosus*, or whether these important subtidal predators avoid the invasive prey, a situation that could subsequently facilitate further spread of *S. algosus*.

METHODS

Specimen collection and maintenance

The 4 mussel species used in this study were sampled from monospecific mussel beds along the west coast of South Africa (between 33°49'S, 18°28'E and 34°02'S, 21°38'E). Starfish and rock lobsters were collected from subtidal sites on the south coast and then used in trials in 2015 and 2016, respectively. As *S. algosus* has only recently (ca. 2015) spread to the south coast, these sites were selected, as native predators along the south coast are not considered to have been exposed to this prey for a substantial period of time. For all experiments, mussel size ranged within 20–30 mm. In rock lobster trials, individuals with carapace lengths of 65–75 mm were used and in starfish trials, individuals with arm lengths that ranged within 50–80 mm were used. These size ranges were selected as previous work has established preferred prey size

Table 1

Diet treatments offered to rock lobsters and starfish, with "Pre-invasion" and "Post-invasion" diets reflecting the more recent invasion of the mussel *S. algosus*

	Mussel Composition			
Diet	*A. atra* (native)	*C. meridionalis* (native)	*M. galloprovincialis* (invasive)	*S. algosus* (invasive)
Baseline	6	6	6	6
Pre-invasion	6	6	12	0
Post-invasion	3	3	9	9

The numbers in the table reflect the number of mussels offered per species per diet.

matching for both lobsters (Griffiths and Seiderer 1980) and starfish (Penney and Griffiths 1984).

Upon collection, all specimens were returned to the laboratory at Stellenbosch University and maintained in holding tanks with aerated artificial seawater at a salinity of 30–35 ppt. and at a constant temperature of 15 °C. Water changes were carried out daily for predators, and twice daily for mussels. Mussels were supplied with algal culture every two days prior to experiments. In order to standardize hunger levels across all replicates, rock lobsters and starfish were starved for a period of seven days prior to experiments. However, during trials starfish took longer to commence feeding (ca. 20 days), which could be an indication that they require a longer period of time to become acclimatized to laboratory conditions, or that a longer starvation period might be needed as a result of their comparatively slower feeding rates (Penney and Griffiths 1984).

Feeding trials

Feeding trials were conducted separately for individual lobsters and starfish. Lobster trials were undertaken in tanks with bases measuring 40 × 27 cm and filled with 11 L seawater whereas starfish trials took place in circular tanks of 23 cm diameter filled with 5 L seawater. Individual rock lobsters and starfish were presented with one of 3 diet treatments consisting of the four mussel species scattered haphazardly on the floor of the tank in varying proportions that represented different mussel invasion scenarios (Table 1). "Pre-invasion" and "Post-invasion" diets provided reference to the invasion of *S. algosus*, with the "Baseline" diet simply consisting of equal proportions of all prey species (Table 1). To account for potential differences driven by the sex of lobsters (Mayfield et al. 2000a), every diet treatment was replicated nine times each for males and females, with the exception of the "Baseline" diet where logistical constraints resulted in only eight replicates for males. Lobsters respond rapidly to visual cues (Hirtle and Mann 1978) and, as such experiments were monitored only once daily to avoid possible disturbances that could interfere with normal feeding behavior. Lobsters that molted during the acclimatization period or during trials were not used in experiments. Experiments with lobsters were run for a total of 10 days. In starfish trials, 9 replicates of each of the 3 diets were employed (Table 1). However, due to their comparatively slower feeding rate (Penney and Griffiths 1984), starfish trials ran for a total of 40 days.

Monitoring of experiments for both predators consisted of the identification, removal, and replacement of consumed mussels in order to maintain constant proportions of the respective diets throughout experiments. Controls for both the predator experiments were 3 replicates of each diet containing mussels in the absence of any predator to confirm that mussel mortality during trials was attributable to predation and not due to other confounding factors.

Chesson selectivity index

The Chesson selectivity index was used in order to assess the prey preference of lobsters and starfish towards the mussel species across the 3 diets (Chesson 1978). Selection toward particular species of prey was determined through the equation:

$$\alpha_i = \frac{(r_i / p_i)}{\sum_i (r_i / p_i)}; i = 1, \ldots, n$$

where r_i is the percentage of a particular species in the diet (consumed), p_i the percentage of that same particular species in the overall habitat (on offer) and n the total number of mussel species in the overall habitat (on offer). When $\alpha = 1/n$ the absence of selective predation is indicated, whereas $\alpha < 1/n$ infers negative selection (avoidance) and $\alpha > 1/n$ infers positive selection (preference). The use of this particular selectivity index is justified as it takes into account the presence of other prey items, thus incorporating the presence of multiple species (and in varying proportions) that are present in the overall habitat of the predator.

Assessments of prey preference indices for both rock lobsters and starfish were undertaken with repeated measures ANOVAs. For lobsters, "diet" and "sex" were employed as between factors, and index for each mussel species as a within factor. For starfish, "diet" was designated a between factor and index for each mussel species as a within factor. Data were arcsine transformed prior to statistical analyses. All analyses were carried out in SPSS (Version 24.0; IBM, 2016).

Mussel morphology and energetic content

To investigate some of the underlying factors that could explain prey preference, several characteristics of the prey species were assessed. These included among species differences in 1) shell strength that can mechanically limit the ability of lobsters to crush mussels (Juanes 1992), 2) adductor muscle size that may influence opening of mussels by starfish (Reimer and Harms-Ringdahl 2001), and 3) energetic content that may make particular species more sought after by predators (Creswell and McLay 1990). Ten individuals of each mussel species from the size class utilized during the feeding experiments were used to compare morphometric characteristics and total energy and were collected from the same sites as those used in the feeding trials.

Shell strength was measured using a Zwick 1484 universal tensile tester and pressure was applied at a rate of 2 mm s^{-1}. Shells were separated and the point of fracture was established for both valves, the average of which was used as a representation of individual mussel shell strength (Mackenzie et al. 2014). All shells were orientated in the same way during testing i.e. the shell length along the horizontal axis of the instrument with the outer shell facing upwards. The size of adductor muscles was determined by weight (Reimer and Tedengren 1997). After collection, posterior adductor muscles were separated from the rest of the flesh and dried to a constant weight at 60 °C, after which they were weighed to the nearest 0.01 mg. Energetic content (kJ/individual) was determined by the equation: mean kJ/g x dry flesh weight (g). This was determined by removing the flesh from mussels and drying samples to a constant mass at 60 °C to gain the dry flesh weight for each

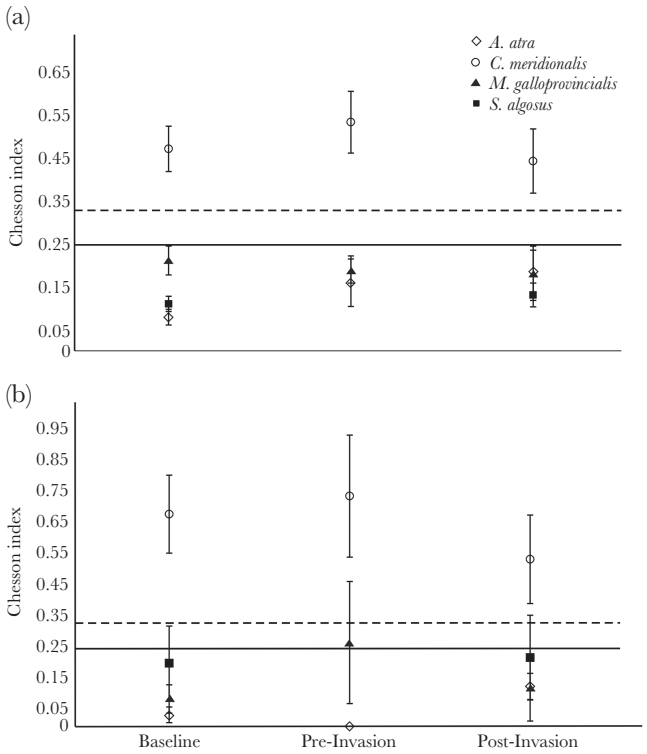

Figure 1
Chesson selectivity indices (±SE) for 4 mussel species as offered in the 3 "diet" treatments to (a) rock lobsters *Jasus lalandii* (males and females grouped) and (b) starfish *Marthasterias africana*. For "Baseline" and "Post-invasion" diets, values above solid line = positive selection. For "Pre-invasion" diet, values above dashed line = positive selection. Values below lines are indicative of avoidance and values on lines of neutral selection. Empty shapes = native species; filled shapes = invasive species.

individual. Samples were then ground into powder form and the energy content (kJ/g) was determined by bomb calorimetry. This measure was then used to determine the energetic content per individual. Both morphometric characteristics and energetic content were compared among mussel species using a one-way ANOVA followed by Tukey's HSD test.

RESULTS

Control experiments without predators had 100% mussel survival. Therefore, mussel mortality in feeding trials with lobsters and starfish was considered to be as a result of predation.

Rock lobsters

No significant differences in mussel consumption were detected between male and female lobsters in the "Baseline" diet ($F_{3, 45} = 3.45$, $P = 0.061$), "Pre-invasion" diet ($F_{2, 32} = 1.424$, $P = 0.256$), or the "Post-invasion" diet ($F_{3, 48} = 0.288$, $P = 0.834$). Repeated measures ANOVAs considering the Chesson selectivity indices for all respective mussel species revealed that there was a significant main effect of mussel species ($F_{3, 150} = 16.574$, $P < 0.001$, Figure 1a). This was driven by stronger selection for the native mussel *C. meridionalis*, as revealed through post hoc pairwise comparisons, where Chesson selectivity indices for *C. meridionalis* compared to other species were significantly different ($P < 0.001$) in all cases. There was no significant effect of "diet" ($F_{2, 50} = 1.969$, $P = 0.15$), and the

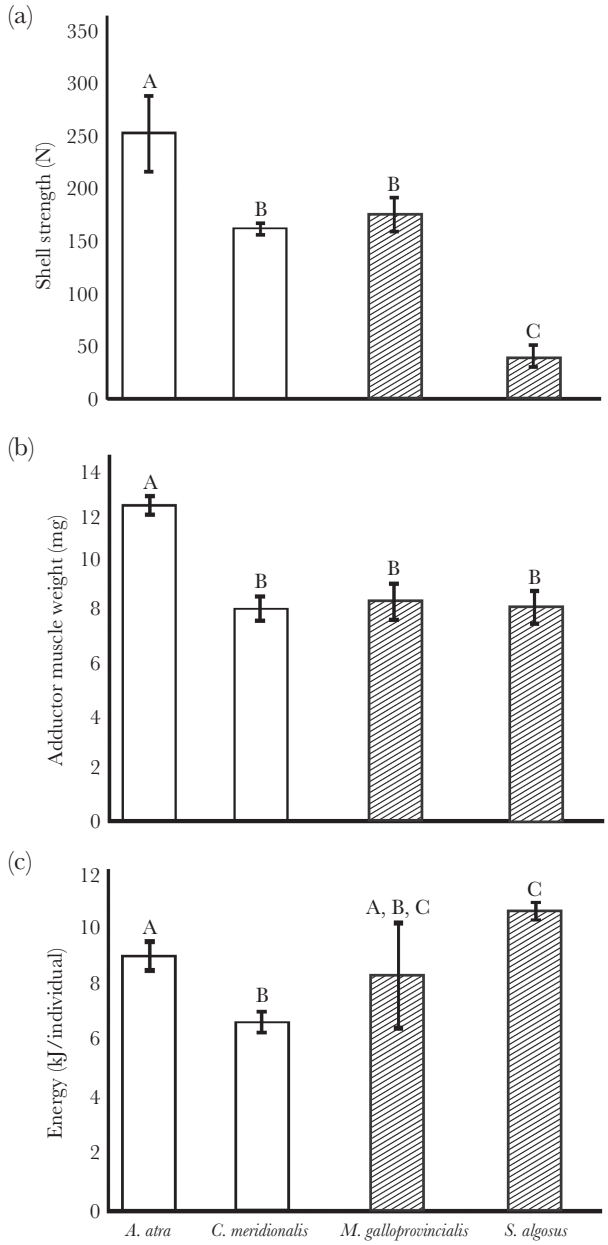

Figure 2
Mean (±SD): (a) shell strength, (b) adductor muscle weight, and (c) energetic content (±SE) of the native mussels *Aulacomya atra* and *Choromytilus meridionalis* (empty bars) and the invasive mussels *Mytilus galloprovincialis* and *Semimytilus algosus* (filled bars). Bars not sharing common letters are significantly different (Tukey's HSD test, $P < 0.05$).

"diet" × "prey" interaction was also non-significant ($F_{6,150} = 1.005$, $P = 0.42$). It was notable that rock lobsters consumed all the flesh of mussels that they opened, suggesting that acceptance or rejection of prey was decided before consumption began.

Starfish

Repeated measures ANOVAs assessing the Chesson indices revealed a significant main effect of prey species ($F_{3, 15} = 11.323$, $P < 0.001$, Figure 1b). Posthoc pairwise comparisons revealed that this was driven by a significantly greater selection of the native mussel *C. meridionalis* compared to the other mussel species ($P < 0.001$ in all

cases). Similarly to lobsters, starfish consumed all mussels that they opened.

Mussel morphology and energetic content

Shell strength was found to vary among mussel species (F_3 = 179.580, P < 0.001) with the native mussel *A. atra* demonstrating the highest mean shell breaking force (252.7N ± 36.04 SD) (Figure 2a). No difference in shell strength was found between *M. galloprovincialis* (174.7N ± 16.19) and *C. meridionalis* (161.1N ± 5.45), while the emerging alien *S. algosus* had the weakest shells (41.2N ± 10.46). The size of adductor muscles also varied among species (F_3 = 121.465, P < 0.001) and was driven by *A. atra* having significantly larger muscles than all other species (Figure 2b). There was a significant difference in energy offered by the four mussel species (F_3 = 13.92, P < 0.001). Notably, the mean energy content of *S. algosus* individuals (10, 5 kJ ± 0.3 SE) was significantly greater than both native species *A. atra* (8.8 kJ ± 0.5) and *C. meridionalis* (6, 6 kJ ± 0.38; Figure 2c), while the preferred native species *C. meridionalis* had the lowest energy, differing significantly from all species except *M. galloprovincialis* (Figure 2c).

DISCUSSION

Invasions by alien species can result in the displacement of native species (Crooks 2002; Shinen et al. 2009), leading to dramatic changes in the availability of native prey as a resource for predators (Carlsson et al. 2009). Native predators that are able to switch from feeding on native prey to novel invasive prey may unlock an abundant new food source (Barber et al. 2008). However, there is also the possibility that predators may avoid novel invasive prey due to unfamiliarity, and may continue to select and consume native species, despite a potentially greater availability of the novel resource (Carlsson et al. 2009; Robinson et al. 2015). This study investigated this phenomenon with regards to 2 native South African subtidal predators, the west coast rock lobster and the spiny starfish, and their selection preferences towards native and invasive mussel prey. Both of these predators demonstrated preference for the same native mussel *C. meridionalis*, even in diet treatments where proportions of the invasive mussels, *M. galloprovincialis* and *S. algosus*, were dominant. These results suggest avoidance of novel prey in both these important consumers, despite them being generalist predators that can be expected to easily incorporate novel prey into their diets (Rodriquez et al. 2006; Carlsson et al. 2009).

The avoidance of both the invasive mussel species by native lobsters and starfish was unexpected. While the avoidance of *S. algosus* by native predators could most easily be explained by unfamiliarity, the avoidance of *M. galloprovincialis* was surprising given the long time period this invasive mussel has been present on the South African coastline (Grant and Cherry 1985). However, fieldwork conducted in the same area after the completion of the present study revealed that, despite the intertidal dominance of *M. galloprovincialis* (Robinson et al. 2005), this species was virtually absent from subtidal sites from which predators were collected (Skein, unpublished data). In fact, *M. galloprovincialis* was recorded from only one site during extensive subtidal surveys representing less than 4% of mussels present. This suggests that despite the well-established presence of this invader in intertidal habitats, subtidal predators may in fact not have encountered it and may consequently be unfamiliar with feeding on this prey.

Nonetheless, to confirm that avoidance of the invasive mussels by lobsters and starfish was in fact the result of unfamiliarity, it is important to consider other factors that may affect prey choice by predators. In this study, comparisons of shell strength revealed that the invasive mussels *M. galloprovincialis* and *S. algosus* do not have stronger shells than the native mussel species. In fact, *S. algosus* had the weakest shells of all four species but was still not selected for by lobsters, despite them crushing mussel shells to access their prey. Starfish utilize a different approach to handling prey and pry open mussel prey. However, the avoidance of the invasive mussels by these predators could not be explained by adductor muscle strength, as the invasive mussels did not have larger adductor muscles than the native mussels. It is interesting to note that the avoidance of the native *A. atra* by lobsters is likely reflective of its strong ribbed shell. Previous comparative studies of the native mussels *A. atra* and *C. meridionalis* have illustrated that a larger force is required by rock lobsters to crush and detach *A. atra* than *C. meridionalis* of equal lengths (Griffiths and Seiderer 1980), and this, coupled with a high level of unfamiliarity towards the invasive mussels, is a potential mechanism behind the preference toward *C. meridionalis* observed in this study. Similarly, the selection for *C. meridionalis* by starfish likely relates to the larger adductor muscles of *A. atra*, which together with avoidance of *M. galloprovincialis* and *S. algosus* drives the choice for *C. meridionalis*.

A primary driver of prey choice is the ability of predators to handle prey and effectively access the energetic reward they offer (Hughes and Dunkin 1984). In this case, *C. meridionalis* in fact offers the lowest reward in terms of energetic content, a finding that aligns with a previous intertidal study that compared *C. meridionalis*, *A. atra*, and *M. galloprovincialis* (van Erkom Schurink and Griffiths 1991). This indicates that energetic gain did not govern the predator's selection of prey. It was notable that acceptance or rejection of prey by both predators took place before mussels were opened. This, together with findings on shell strength, adductor muscle size, and energetic content, suggests that prey choices by these predators may reflect one of 2 scenarios; 1) unfamiliarity with the alien mussels or 2) prey choice may not be governed by the traditional optimal foraging theory framework that assumes prey is selected in a way that maximizes energetic gain. Recent research suggests that some predators might not forage to optimize net energetic gain, but rather manage the intake and balance of macronutrients (Machovsky-Capuska et al. 2016). It has been suggested that various fitness-related aspects (e.g. egg production (Jensen et al. 2012), longevity (Lee et al. 2008), immunity (Le Couteur et al. 2015)) are linked to the ability of predators to actively select for particular nutrients while foraging. In order to determine whether the predators studied here are foraging in this way, additional studies that consider the nutritional composition of different prey species would be required. However, it is unlikely that taxonomically different organisms such as rock lobsters and starfish have the same nutritional requirements, given the large differences in their physiology and life histories. As such, the selection and avoidance of similar prey species by both predators is probably explained by the unfamiliarity of avoided prey rather than by prey nutritional composition. As *S. algosus* is thought to only recently have invaded the south coast, we suggest that the most likely explanation for our results is unfamiliarity. However, if this species did invade earlier, it is possible that subtidal predators might have had previous exposure to this prey and drivers of prey selection that were not considered in this study may be at play.

Positive selection towards *C. meridionalis* occurred across all diet treatments, even when proportions of other species were greater. This was an unexpected finding given the broad diets of the

predators in the study (Barkai and Branch 1988a, b; Edgar 1990; Mayfield and Branch 2000; Mayfield et al. 2000a) and discounted our a priori hypotheses. It has been suggested that generalist predators, such as rock lobsters and starfish, switch to alternative prey as the density of their main prey declines (Reif et al. 2001; Kjellander and Nordström 2003). According to the alternative prey hypothesis (Angelstam et al. 1984), the predation pressure on such an alternative should increase as the density of the most selected prey decreases (Pöysä et al. 2016). The results of this study demonstrate, however, that both predators continue to select *C. meridionalis* even in instances when it is the least abundant prey species. If this was to occur in the field, then predatory forces may contribute to increased pressure on populations of this species. The positive selection towards *C. meridionalis* demonstrated by both rock lobsters and starfish may in fact facilitate the continued invasion of the non-native mussel species. By increasing the availability of primary rock space through predation of native competitors, these predators might be removing potential barriers for further invasive spread (Needles et al. 2015). The fact that *S. algosus* has spread more than 350 km along the open coast in just eight years (Robinson, unpublished data) may well be reflective of such facilitation.

This does not present the first observation of native predators failing to select for invasive prey (e.g. López et al. 2010; Veiga et al. 2011). However, in other cases, the avoided invasive prey were suggested to possess physical characteristics that might hinder predation from native predators. In contrast, this study found that alien prey were unlikely to offer predators such constraints. Additionally, we demonstrate that two important native predators, select for native over invasive mussel prey species despite the fact that they were offered in reduced proportions. In the broader context, these findings highlight that predator-driven biotic resistance may not manifest, even in the context of generalist predators. Importantly, when such prey avoidance coincides with selection of native prey that may have offered invasion resistance through inter-specific competition, native predators may indirectly facilitate invasions. While it is presently unclear how often such facilitation acts, interrogating the behaviors that drive such outcomes will advance our understanding of successful invasions.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Skein et al (2017).

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